Patterns of lake occupancy by fish indicate different adaptations to life in a harsh Arctic environment

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SUMMARY

1. For six fish species sampled from 86 lakes on the Arctic Coastal Plain, Alaska, we examined whether lake occupancy was related to variables representing lake size, colonisation potential and/or the presence of overwintering habitat.

2. We found the relative importance of each factor for a given species could be related to its ecology and adult size. The three large-bodied migratory species, least cisco (*Coregonus sardinella*), broad whitefish (*Coregonus nasus*) and arctic grayling (*Thymallus arcticus*), were influenced by factors associated with the likelihood of fish recolonising lakes, including whether the lakes had a stream connection. Of the large-bodied species, least cisco had the highest likelihood of occupancy (0.52 ± 0.05) and models provided evidence that least cisco exhibit both migratory and resident forms.

3. Models for small-bodied fish differed among species, indicating different niches. Ninespine stickleback (*Pungitius pungitius*) were the most widespread and ubiquitous of the species captured (occupancy probability = 0.97 ± 0.01); they were captured in lakes that freeze to the bottom, suggesting that they disperse widely and rapidly after the spring freshet, including colonisation of sink habitats. Alaska blackfish (*Dallia pectoralis*) had a lower occupancy (occupancy probability = 0.76 ± 0.05) with a distribution that reflected tolerance to harsh conditions. Slimy sculpin (*Cottus cognatus*) had an occupancy probability of 0.23 ± 0.06, with a distribution indicating its marine origin.

4. Based on these patterns, we propose an overall model of primary controls on the distribution of fish on the Arctic Coastal Plain of Alaska. Harsh conditions, including lake freezing, limit occupancy in winter through extinction events while lake occupancy in spring and summer is driven by directional migration (large-bodied species) and undirected dispersal (small-bodied species).

Keywords: Alaska, Arctic lakes, connectivity, landscape, occupancy modelling

Introduction

Patterns of habitat occupancy are a consequence of the relationship between species traits and the habitat features that limit their distribution (Poff, 1997). The distribution of fish may be affected by historical constraints (e.g. glaciation; Oswood *et al.*, 2000), barriers to local colonisation (Spens, Englund & Lundqvist, 2007) or factors that promote recruitment and overall population persistence (Salonen *et al.*, 2009). At regional scales, the distribution of fish is shaped by climate, large-scale barriers to dispersal and historical biogeographical influences (Tonn *et al.*, 1990). At finer spatial scales, distribution is influenced by the extent, shape and abiotic features of the habitat, the structure of the surrounding landscape and biological factors (e.g. competition and predation; Jackson, Peres-Neto & Olden, 2001). Controls on fish distribution are complex and act on a number of scales.

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However, this complexity can be alleviated in situations where the system is well studied or has a single dominant factor (e.g. hypoxia, severe cold) that simplifies the number of filters determining assemblage composition.

Arctic lakes provide an excellent opportunity to examine how environmental features affect the distribution of fish and how species are adapted to a harsh and dynamic environment. Compared with other aquatic systems, lakes are isolated (Magnuson, 1976) and can be examined as discrete patches with a limited number of environmental influences. Biologically, Arctic lakes are relatively simple because of low species diversity and productivity, and because species have physiologically and geographically constrained distributions (Hershey et al., 1999). Further, these systems are less affected by anthropogenic influences that complicate ecological study, including heavy fishing pressure, pollution, introduction of non-native species, transfer and stocking of native species and alterations of waterways.

Fish assemblages on the Arctic Coastal Plain (ACP) are largely recruited from the fauna of the Beringian refugia, but also include species that took advantage of Pacific Coast or Mississippi Pleistocene refugia (Oswood et al., 2000). At finer spatial scales, species-specific responses to landscape controls, like colonisation potential and the presence of local refugia, are likely to be reflected in differences in distribution patterns among species (Jackson et al., 2001). Fishes on the ACP have diverse morphologies and ecologies, including major life-history traits such as reproductive timing and investment, migratory patterns and trophic position (Reynolds, 1997; Hershey et al., 1999). Species also differ in their ability to persist in lakes and to colonise new lakes. These differences among species traits probably drive the variation in occupancy among fishes on the ACP.

There are relatively few descriptions of the distribution of fish on the ACP and elsewhere in the Arctic. Two notable studies include Hershey et al. (1999), who suggested a geomorphic–trophic conceptual model of the distribution of Arctic fish, and Hershey et al. (2006), who provides empirical models of fish distributions in lakes in relationship to landscape features. Both these studies were restricted to an area (18 000 km^2) in the foothills of the Brooks Range Mountains, which differs from most of the ACP in terms of fish species composition and abundance, landscape features and topography, geomorphic constraints and glaciation history (Oswood et al., 2000). To improve our understanding of the distribution of lacustrine fish in the Arctic, we investigated the occupancy of six species across a broad northerly area of the ACP. We examined three large-bodied

species, least cisco (Coregonus sardinella), broad whitefish (Coregonus nasus) and arctic grayling (Thymallus arcticus), and three small-bodied species, ninespine stickleback (Pungitius pungitius), Alaska blackfish (Dallia pectoralis) and slimy sculpin (Cottus cognatus). These species vary in their ecological attributes and life histories, which can lead to species-specific responses to spatial and temporal variation in environmental conditions (Winemiller & Rose, 1992) and, ultimately, variation in lake occupancy (Miyazono et al., 2010). We expected that local and regional features relating to local persistence and colonisation potential in lakes would determine fish occupancy; however, the scale and strength of the effects would depend on the biology of the individual species, including their dispersal and migratory capabilities and tolerance to winter conditions. Our overall goal was to provide a conceptual model of primary controls on the distribution of fish in Arctic lakes, contrasting the effects of landscape connectivity and overwintering refugia on fish species that vary in body size, tolerance to winter conditions and ecology.

Methods

We sampled 86 lakes for fish over a large area (c. 8500 km^2) of the ACP located within the National Petroleum Reserve – Alaska. We focussed on lakes in 16 plots, each 7×7 km in dimension, randomly distributed across the study area (Fig. 1). Within a plot, we selected lakes with a surface area >7 ha, at random except that half were occupied by piscivorous yellow-billed loons (Gavia adamsii) and half not.

We began sampling on 4 July 2009 and 23 June 2010, shortly after the spring freshet (when snow and ice had melted rapidly and caused widespread flooding) and continued until mid-August, encompassing the growing season for fish. Three sampling crews (two-four people in each) worked independently on separate lakes throughout the season. Crews sampled each lake during a single visit of 48–72 h before moving to the next lake. We used five methods to sample the fish, including gill-nets (two nets, three replicates net^{-1}), minnow traps (eight traps, two replicates trap^{-1}), fyke nets (two nets, two replicates net^{-1}), dip nets (one net, 30 replicates net^{-1}) and beach seines (one net, two replicates net^{-1}). Samples were replicated spatially (several sets of the same gear sampling at the same time) and temporally (a single set of gear used a number of times). For example, we used two fyke nets (two spatial replicates), each checked twice (two temporal replicates) for a total of four replicates per lake. Because our temporal replication
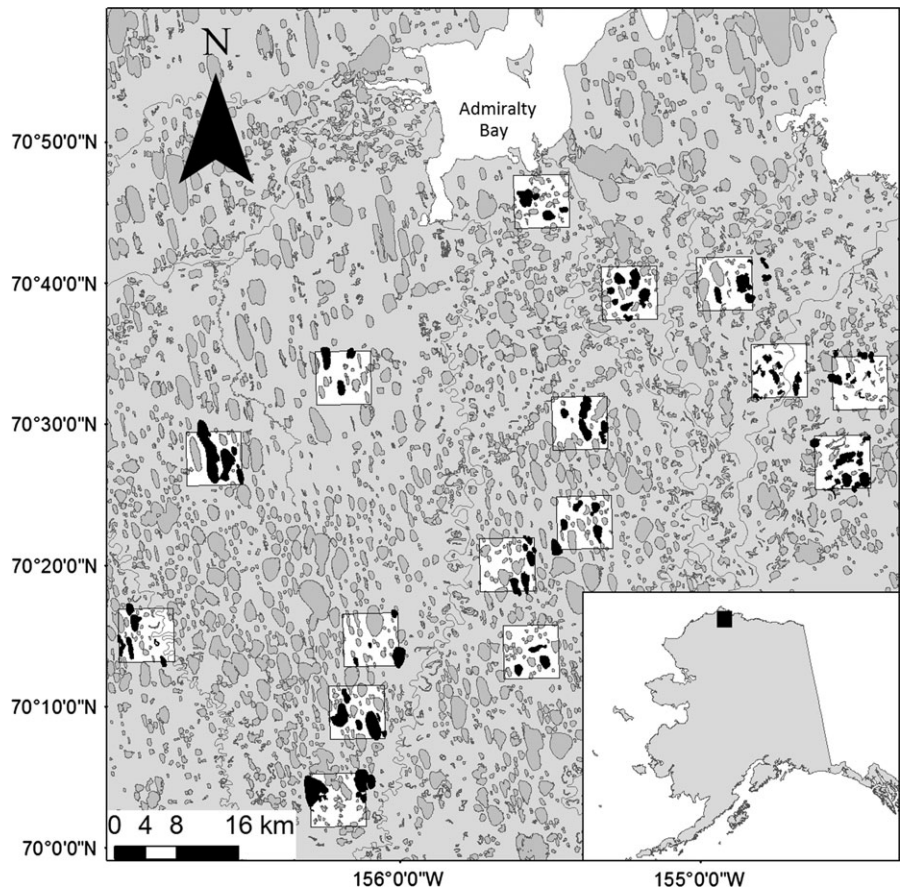
Fig. 1 Study area on the Arctic Coastal Plain, with inset map of Alaska showing the study region (black box). White squares represent 7 × 7 km sample plots, and study lakes are shown in black.

took place over a short period (i.e. <72 h), it is unlikely that we violated the site-closure assumption for occupancy modelling (MacKenzie *et al.*, 2006). We generally deployed fyke nets and minnow traps before midday and conducted beach seine, dip net and gill net sampling throughout the afternoon. Although there was some variation in the timing of gear deployment, our previous work suggested that there were no strong diurnal effects on gear sampling efficiency (Haynes *et al.*, 2013). Methods used for each gear type are described below and in greater detail in Haynes *et al.* (2013).

Gill nets

We used two variable-mesh gill nets measuring 38 m × 1.8 m with five panels ranging in mesh size from 1.3 to 6.5 cm. We checked gill nets every two to three hours, then removed the nets after the third check.

Minnow traps

We baited eight Gee-style galvanised steel minnow traps (2.5-cm opening with 6-mm mesh) baited with preserved salmon eggs and generally deployed traps before midday. We deployed four traps individually in shallow water along the shoreline ('shore minnow traps') and sunk four traps in deepest zone of the lake ('benthic minnow traps'). Shore and benthic minnow traps had different probabilities of catching fish and were therefore considered as two separate methods (Haynes *et al.*, 2013). We checked traps after 12 h, rebaited and replaced them, and checked and pulled them after 24 h.

Fyke nets

We sampled shorelines with two fyke nets, each with 15.2 × 1.2 m wings and a 30.5 × 1.2 m centreline with 0.6-cm-sized stretched mesh. Wings and centreline had float lines and weighted lead lines. The hoop net was constructed of 0.3-cm-sized stretched mesh and had a frame opening of 1.1 × 1.1 m, followed by five sequential hoop frames spaced 0.8 m apart and measuring 0.6 × 0.6 m in size. The hoop net had three net throats within the frame measuring 15 × 23 cm at the middle of each throat. We checked nets twice for fish, once after about 12 h and again after 24 h when we removed the nets.

Dip nets

We swept dip nets (3-mm mesh; two opening sizes 28 × 38 × 20 and 41 × 41 cm) along the lake bottom adjacent to the shore for three eight-minute intervals and identified and counted fish for each interval.

Beach seine

We employed a 3-mm mesh beach seine measuring 15 m in length that tapered in width from 3 m at the middle to 1.2 m at the wings. We conducted two beach seine replicates, covering approximately 10–15 m in length. The second replicate was offset from the first by at least 5 m parallel along the shore.

Environmental variables

For hypothesis testing and model development, we categorised environmental variables (Table 1) based on proposed ecological mechanisms determining the distribution of fish, including patch size (one variable), directional migration (five variables), undirected dispersal (four variables) and persistence (two variables). Variables were evaluated and quantified at two spatial scales: local (the scale of the sample lake) and regional (the mean value of the variables from lakes within the boundaries of a set of 7 × 7 km plots gridded across the study area). Although we measured water quality variables (dissolved oxygen, temperature, pH, specific conductivity) on most lakes, we did not consider these variables in analyses because lakes varied little in water chemistry (as also noted by Hershey *et al.*, 2006).

Patch size can represent the amount and diversity of habitat available to a species. Small lakes, like small islands (MacArthur & Wilson, 1967), may have lower colonisation rates simply due to their size. We expected patch size to be important for all species, especially resident species. We calculated the patch size as the lake surface area ('L_LakeArea').

Swimming aquatic organisms require hydrologic connections between lakes to disperse (De Bie *et al.*, 2012). For lakes, colonisation potential can be influenced by environmental features that promote directional migration (i.e. movement to a specific location) or undirected dispersal (i.e. movement with no specific destination). The importance of directional migration versus undirected dispersal for fish depends on species. We predicted that the 'occupancy probability' (the probability of a species being present in a lake) for large-bodied species would be influenced by directional migration over relatively long distances along migratory pathways from overwintering habitats (river systems and estuaries) into lakes in the summer for breeding. We considered the following variables as likely influences on colonisation potential along migratory pathways: hydrologic connectivity (both local and regional), regional lake area and regional measures of the distance to the coast and to the nearest river. We defined local hydrologic connectivity ('L_Connect') as the existence of a surface waterway (generally a stream) connecting a focal (surveyed) lake to another waterbody (stream, river, lake, pond or wetland). We determined whether a lake had a connection during the summer by a combination of observations of a digital map (i.e. National Hydrography Dataset), aerial photographs and ground observation

Table 1 Description of environmental covariates considered in the analysis of occupancy probabilities for fish species on the Arctic Coastal Plain, Alaska

Covariate	Scale	Abbreviation	Ecological relevance*	Range[†]
Lake area	Local	L_LakeArea	Local patch size	0.2–14.9 km^2
	Regional	R_LakeArea	Directional migration	5.0–27.9 km^2
Hydrologic connectivity	Local	L_Connect	Directional migration	0–1 (binary)
	Regional	R_Connect	Directional migration	2.9–66.1 km
Distance to river	Regional	R_DistRiver	Directional migration	0.3–13.0 km
Distance to coast	Regional	R_DistCoast	Directional migration	5.5–83.0 km
Altitudinal gradient	Local	L_Grad	Undirected dispersal	−0.4–1.7 m
	Regional	R_Grad	Undirected dispersal	0.3–1.3 m
Lake distance	Local	L_DistLake	Undirected dispersal	16–657 m
	Regional	R_ DistLake	Undirected dispersal	47–263 m
Winter refugia	Local	L_RefArea	Persistence	0–96%
	Regional	R_RefArea	Persistence	0–61, 623 km^2

*Ecological relevance – the perceived ecological influence of covariates on fish occupancy.
[†]We standardised all continuous variables into *z*-scores (mean = 0, SD = 1) before analysis.

(truthing). Regional connectivity ('R_Connect') is a measurement of the total linear distance (km) of streams and rivers at the regional scale (i.e. within a 7 × 7 km grid). Lakes may provide stepping stones for fish migration, and we calculated regional lake area ('R_LakeArea') as the mean L_LakeArea at the regional scale. We measured the distance to the nearest river ('R_DistRiver') or to the north coast ('R_DistCoast') as the shortest linear distance to the feature from the centroid of the 7 × 7 km grid cell.

We predicted that lake occupancy by resident, small-bodied species would be influenced by variables related to undirected dispersal (i.e. variables that may promote general dispersal, with no specific destination). Variables considered to relate to undirected dispersal included regional and local measures of altitudinal gradient and distance among lakes. These variables may affect dispersal ability during the spring freshet, when low lying flood waters can create temporary pathways for dispersal. As a measure of local altitudinal gradient ('L_Grad'), we used the mean value of the lake altitude relative to the minimum value within a set of 'buffer zones' (5–10 m, 10–25 m, 25–100 m) around the lake perimeter (Gross, Jones & Arp, 2013). The regional altitudinal gradient ('R_Grad') was calculated as the mean L_Grad at the regional scale. We measured local distance between lakes ('L_DistLake') as the distance of the sample lake to the next closest lake >7 ha in surface area. We calculated the regional distance between lakes ('R_DistLake') as the mean value of L_DistLake at the regional scale.

Lake depth can be an important driver of fish distributions on the ACP through its influence on the persistence over winter of resident fish. The ACP has extremely cold winters during which much of the water becomes frozen. When stream and river connections freeze, it restricts fish movements and isolates fish populations within the lakes. Lakes may partially or completely freeze, depending on the water depth (generally depths <1.6–2.2 m freeze to the bottom; Jeffries, Morris & Liston, 1996; Grunblatt & Atwood, 2014). When shallower lakes freeze partially to the bottom, fish habitat within that lake becomes restricted, and this can reduce or eliminate local populations due to anoxia in liquid water under the ice. If the entire lake freezes, local extinction occurs. Synthetic aperture radar (SAR) satellite imagery shows strong differences in signal between ice extending to the lake bed and ice with liquid water beneath (Jeffries *et al.*, 1996). We used SAR modelled data of the proportion of the lake (by surface area) that does not freeze to the bottom (Grunblatt & Atwood,

2014) to represent the amount of deep, unfrozen water available to fish within a lake. Deep-water refugia can promote survival despite extreme winter or summer temperatures. We predicted that non-migratory (resident) species would have higher occupancy probabilities in lakes with more refugia. The availability of winter refugia (L_RefArea) was calculated as the percentage of the lake surface area that did not freeze to the bottom during winter, as inferred from SAR imagery collected in late winter (April 2009; Grunblatt & Atwood, 2014). Regional availability of winter refugia (R_RefArea) was calculated as the sum of the lake surface area that does not freeze to the bottom during winter from all lakes within each 7 × 7 km grid cell.

Data analysis

We used occupancy modelling and an information theoretic approach to model selection to estimate occupancy probability and to examine whether specific environmental covariates affected it. For each pair of variables showing a high degree of colinearity (correlations ≥0.70; Berry & Feldman, 1985), we removed the variable that showed the highest correlation with others in the set. This excluded R_LakeArea (correlated with R_RefArea) and R_Connect (correlated with R_DistCoast) from further analysis. We created a set of *a priori* models in the program PRESENCE (Version 5.7; Hines, 2006) using the single-season, multimethod occupancy modelling parameterisation (Nichols *et al.*, 2008). Although we had two years of data, we did not sample any site in both years so we could not use a multiseason approach. Haynes *et al.* (2013) explicitly examined detection for these data and found cumulative detection probability to be high and to vary by sampling method, lake area, relative lake depth (inferred by SAR imagery), day and year. We used the detection probability structure from Haynes *et al.* (2013) to examine occupancy by allowing detection probability to vary by sampling method and four site covariates: L_LakeArea, L_RefArea, Day and Year, where Day was the number of days from the beginning of sampling and Year was binary (representing 2009 or 2010).

We constructed separate candidate model sets for each species to determine whether its occupancy was associated with variables categorised by their spatial scale (local or regional scales) and perceived ecological relevance, including patch (lake) size, directional migration or undirected dispersal (affecting colonisation potential) or overwinter habitat variables (affecting population persistence). We used a two-step approach to reduce the number of candidate models in the model set. First, for

each variable category (4), we ran combinations of variables based on scale (local versus regional versus local plus regional variables) and ranked these in the overall model set, including a saturated and a null model (18 models). Using the highest-ranked variable combination for each category determined from the previous step, we ran combinations of variables, grouped by category (e.g. directional migration and overwinter habitat), for all category combinations that remained (11 models). For example, based on the competing model set within each category, a species may be found in the first step to be influenced by L_LakeArea for patch size; L_Connect for directional migration; L_Grad, R_Grad and R_LakeDist for undirected dispersal; and L_RefArea for overwintering habitat. In the second step, all combinations of models from the four categories competed against each other (if more than one variable was important for a category, then those variables were entered together). The hypothetical species in the example above may have the top model in the second step include variables representing patch size and undirected dispersal, giving a top mode with the following covariates for occupancy: L_LakeArea, L_Grad, R_Grad, R_LakeDist.

For each species, we evaluated all models from both steps in the same model set by ranking models using Akaike's information criterion, corrected for sample size (AIC$_c$; Burnham & Anderson, 2002). Determining sample size for occupancy models is still a topic of debate (MacKenzie et al., 2006), and thus, we used the mean value between the number of sites and the number of surveys (least cisco and arctic grayling $n = 683$, broad whitefish $n = 463$, small-bodied species $n = 1284$) to adjust the sample size (MacKenzie et al., 2012). To check for overdispersion, we ran a goodness-of-fit test for each species using the most complex model (MacKenzie & Bailey, 2004). When we found evidence for overdispersion, we adjusted the selection criteria (QAIC$_c$) and sample variances (Burnham & Anderson, 2002). We standardised all continuous covariates by calculating z-scores and did not consider interaction effects for ease of interpretation and parsimony. We eliminated models from the candidate set that did not converge. To adjust for model selection uncertainty, we used model averaging for all models with an AIC weight ≥0.01 to produce parameter estimates and standard errors for beta parameters (Burnham & Anderson, 2002). For each fish species, we examined parameter estimates and standard errors from model-averaged results to determine a covariate's influence on occupancy. We considered variables to be biologically important if they had relatively large effect sizes and precise estimates.

Results

For all species, model estimates of occupancy were very similar to occupancy evident from the raw data ('observed occupancy'), because we conducted a large number of repeated surveys, which produced high cumulative detection probabilities (Haynes et al., 2013). Model selection tables for each species are presented in Supporting Information (Tables S1–S5). Besides the six species we were investigating, we caught eight other fish species with observed occupancies too low to allow for occupancy modelling: Arctic char (*Salvelinus alpinus*; 3/86 lakes), northern pike (*Esox lucius*; 3/86 lakes), rainbow smelt (*Osmerus mordax*; 3/86 lakes), humpback whitefish (*Coregonus pidschian*; 2/86 lakes), three-spined stickleback (*Gasterosteus aculeatus*, 2/86 lakes), Arctic flounder (*Liopsetta glacialis*, 1/86 lakes), fourhorn sculpin (*Myoxocephalus quadricornis*, 1/86 lakes) and burbot (*Lota lota*; 1/86 lakes). Two fishless lakes were sampled during the beginning of the season (day 0 and day 5); these were unconnected and relatively isolated (large local distance between lakes; one lake had a high local altitudinal gradient [L_Grad] value).

The occupancy of least cisco was influenced by variables related to directional migration (L_Connect, R_DistCoast) and suitable habitat within the lake (L_RefArea, L_LakeArea; Fig. 2a,b). Least cisco were more likely to be in lakes connected to streams (logit $\beta_{L\_Connect} = 1.51 \pm 0.62$) and closer to the coast (logit $\beta_{R\_DistCoast} = -1.26 \pm 0.37$). Least cisco occupancy probability increased as a greater percentage of the lake remained unfrozen during winter (i.e. deeper lakes; logit $\beta_{L\_RefArea} = 0.54 \pm 0.34$) and for larger lakes (logit $\beta_{L\_LakeArea} = 0.99 \pm 0.53$). Least cisco had an observed occupancy of 0.51 and an estimated occupancy from the null model of 0.52 ± 0.05.

The occupancy probability of broad whitefish was positively related to directional migration variables (L_Connect, R_DistCoast) and negatively related to the distance between lakes (L_DistLake; Fig. 2c,d). Broad whitefish were more likely to occupy lakes that were connected to streams (logit $\beta_{L\_Connect} = 2.69 \pm 1.38$; Table 2), closer to the coast (logit $\beta_{R\_DistCoast} = -1.24 \pm 0.69$) and close to another lake (logit $\beta_{L\_DistLake} = -0.803 \pm 0.466$). Broad whitefish had an observed occupancy of 0.27 and an estimated occupancy from the null model of 0.31 ± 0.06.

Four of the most complex models of arctic grayling occupancy ($K = 11$–19) failed to converge and were removed from model rankings. Arctic grayling were more likely to be found in lakes that were locally
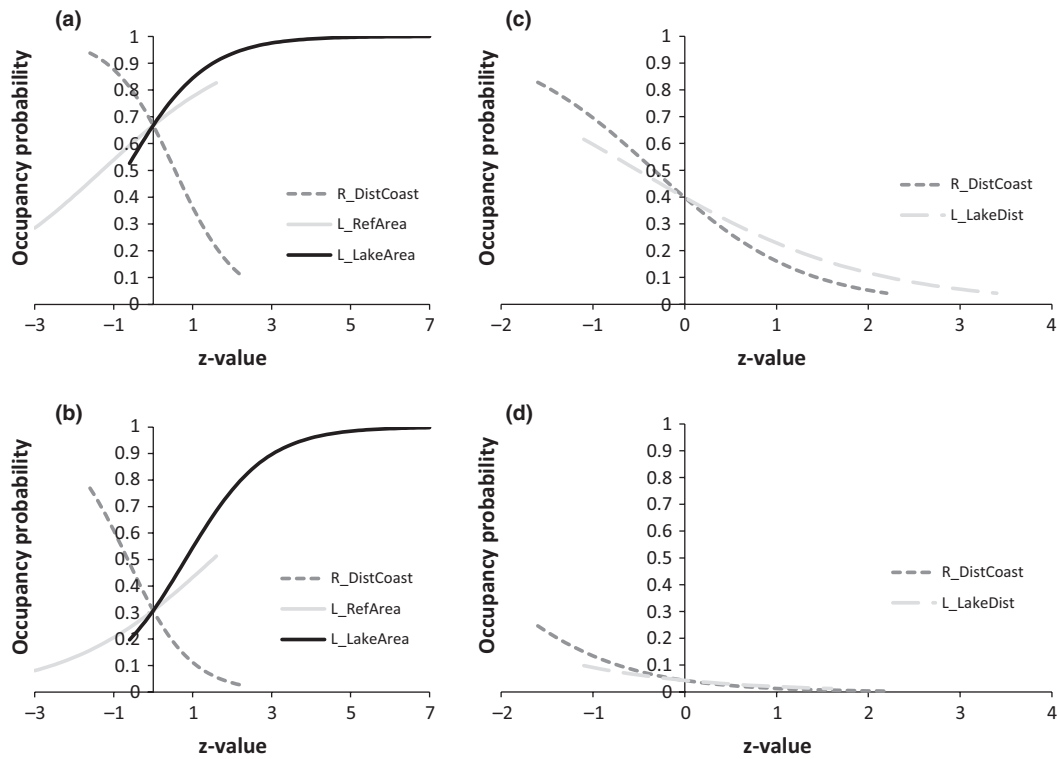
Fig. 2 An example of how the probability of lake occupancy of two fish species [least cisco, (a) and (b); broad whitefish, (c) and (d)] varied in relation to environmental covariates. Covariates important for one or both of these species included distance to the coast (R_DistCoast), per cent of lake that remains unfrozen during winter (L_RefArea) and lake surface area (L_LakeArea), distance to next nearest lake (L_Lake-Dist) for lakes with (a, c) or without a stream connection (b, d). Curves represent the occupancy probability over the standardised (z-value) of the covariates while holding the other covariates at their mean values. The *y*-axis intercept represents the occupancy probability for a site with a connection (a, c) or without a connection (b, d) for the mean values of all continuous covariates.

Table 2 Model-averaged estimates of the untransformed β parameters (± SE) for occupancy models of five fish species occurring in lakes on the Arctic Coastal Plain, Alaska. The ninespine stickleback was omitted because its high occupancy across the study area precluded investigation of relationships between occupancy and covariates

	Small-bodied species		Large-bodied species		
Variable	Alaska blackfish logit β	Slimy sculpin logit β	Least cisco logit β	Broad whitefish logit β	Arctic grayling logit β
R_ DistLake	−0.93 ± 0.35	−0.26 ± 0.42	−0.81 ± 0.81	−1.30 ± 1.50	0.32 ± 0.51
L_RefArea	0.72 ± 0.32	0.60 ± 0.97	0.54 ± 0.34	0.23 ± 0.70	0.26 ± 0.45
L_Connect	0.94 ± 0.86	1.04 ± 1.29	1.51 ± 0.62	2.69 ± 1.38	2.77 ± 1.26
L_LakeArea	0.19 ± 0.37	0.95 ± 1.13	0.99 ± 0.53	−0.91 ± 1.47	0.10 ± 0.38
R_Grad	−0.41 ± 0.50	0.21 ± 0.47	0.39 ± 0.39	−0.27 ± 0.81	−1.18 ± 1.05
L_Grad	−0.33 ± 0.45	0.06 ± 0.37	−0.17 ± 0.36	−0.94 ± 1.16	NA
R_RefArea	0.47 ± 0.57	0.35 ± 0.59	−0.83 ± 0.88	−0.93 ± 0.95	NA
L_ DistLake	−0.30 ± 0.40	0.17 ± 0.35	−0.81 ± 0.81	−0.78 ± 0.57	NA
R_DistCoast	NA	−0.86 ± 0.68	−1.26 ± 0.37	−1.24 ± 0.69	−0.12 ± 0.44
R_DistRiver	NA	−0.38 ± 0.50	−0.05 ± 0.29	−0.01 ± 0.40	0.07 ± 0.44

Models included in the model averaging procedure had an AIC$_c$ weight of 0.01 or greater. 'NA' represents variables that were not included in the models used for averaging.

connected (logit β$_{L\_Connect}$ = 2.77 ± 1.26; Table 2). Grayling were found at 14 of the 86 lakes (observed occupancy = 0.16) and had an occupancy estimate of 0.27 ± 0.09 from the null model.

Ninespine stickleback were found at 83 of the 86 sample sites (observed occupancy = 94%). Because they were found at almost every lake, it was not possible to investigate how covariates influenced occupancy. Based

on the null occupancy model (i.e. no covariates for occupancy), occupancy for ninespine stickleback was estimated to be 0.97 ± 0.01.

We used criteria adjusted for overdispersion ($QAIC_c$) for model selection for Alaska blackfish. Based on the model-averaged results, occupancy of Alaska blackfish was influenced by regional distance among lakes and availability of winter refugia within the lake (Table 2). The probability of occupancy decreased as lakes became less densely distributed at the regional level (logit $\beta_{R\_DistLake} = -0.93 \pm 0.35$) and increased as a greater percentage of the lake remained unfrozen during winter (logit $\beta_{L\_RefArea} = 0.72 \pm 0.32$). Alaska blackfish had an observed occupancy of 0.74 and an estimated occupancy from the null model of 0.76 ± 0.05.

The distance of the plot to the coastline influenced occupancy of slimy sculpin, with probability of occupancy decreasing as distance from the coast increased (logit $\beta_{R\_DistCoast} = -0.86 \pm 0.68$; Table 2). Slimy sculpin were also more likely to occupy lakes that had a stream connection (logit $\beta_{L\_Connect} = 1.04 \pm 1.29$). However, neither R_DistCoast nor L_Connect were estimated with a high level of precision. Observed occupancy was 0.13,

and estimated occupancy from the null model was 0.23 ± 0.06.

Discussion

Lake occupancy by fish was associated with colonisation potential (i.e. variables related to directional migration or undirected dispersal), while other habitat features, such as lake size and the availability of deep-water refugia, were also important for certain species. Broad scale assemblage patterns may depend on whether dispersal rates exceed extinction rates (Shurin, Cottenie & Hillebrand, 2009), especially when local habitat characteristics vary little (Spens *et al.*, 2007) as they do for these Arctic lakes. Given that patch connectivity is increasingly recognised as important in structuring aquatic communities (Fullerton *et al.*, 2010), it is not surprising that colonisation plays a key role in shaping the Arctic fish communities. In the Arctic, hydrologic connectivity plays a primary role in affecting colonisation potential and strongly corresponds to the spatial patterns of resources and organisms (Lesack & Marsh, 2010) including fish (Hershey *et al.*, 1999, 2006). The role of
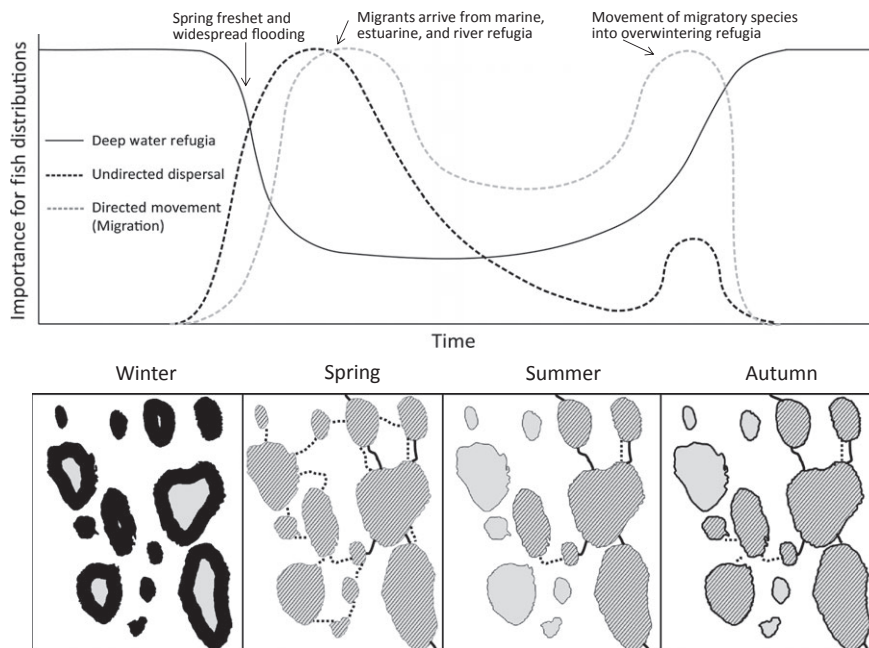

Fig. 3 A conceptual model summarising hypotheses on the environmental drivers of fish occupancy in lakes on the Arctic Coastal Plain, Alaska. During winter, deep-water refugia (in grey) are the primary driver of fish distributions, with ice (black fill) preventing lake connectivity. In spring, rapid thawing increases flooding and lake connectivity (lakes with hashed fill) due to the presence of ephemeral connections (dashed connecting lines) – increasing the importance of undirected dispersal. Permanent connections (solid connecting lines) are important for both dispersal and directed migration, because migrants arrive after spring flooding have receded and ephemeral connections disappear. A pulse of fish movement during late summer/early autumn accompanies the migration of species to river or marine overwintering habitat. In early autumn, ephemeral connections have reformed due to precipitation, increasing the importance of undirected dispersal for lake occupancy prior to winter freeze-up.

colonisation was evident from the importance of local connectivity, whereas the availability of winter refugia (a proxy for persistence potential) was less important than we predicted. However, the relative importance of colonisation and local extinction probably varies seasonally. Because we were examining occupancy after the spring freshet, when fish have already dispersed and colonised new habitats, we found colonisation to be a stronger driver of fish occupancy than factors associated with overwinter survival (persistence).

Based on our findings, we propose a conceptual model of the primary drivers of fish distribution and occupancy on the Arctic Coastal Plain (Fig. 3). At the ecoregional (or hydroregional) scale, distribution and species composition of fish in the Arctic has been shaped by the Pleistocene glaciations (Oswood *et al.*, 2000). At finer scales, the functional relationships between the ecology and life history of individual species and the dynamics of the harsh Arctic environment are the likely determinants of current habitat occupancy. These traits include dispersal capabilities when faced with a seasonally dynamic hydrology (Shurin *et al.*, 2009) and the ability to persist through harsh winters (Jackson *et al.*, 2001). Given that species vary ecologically, we can expect that the influence of environmental characteristics on species occupancy is likely to vary temporally and among species. During the winter, when lakes are covered with ice, deep-water refugia are probably the primary driver of fish distribution, with a lack of refugia resulting in local extinctions (Fig. 3). This is particularly important for resident species that do not migrate out of lakes in the autumn. In this region, Alaska blackfish were widely distributed and ninespine stickleback were almost ubiquitous, suggesting that both these species can tolerate winter conditions. Shallow lakes that freeze to the bottom are likely to lose their fish. However, even in lakes with deep-water refugia, conditions can be harsh enough to cause local population loss (e.g. Danylchuk & Tonn, 2003).

As the winter proceeds and surface ice increases in thickness, the remaining water can be hypoxic, saline (due to the concentration of solutes; Salonen *et al.*, 2009) and very cold. In general, small-bodied species require less oxygen, and both ninespine stickleback and Alaska blackfish can tolerate low oxygen concentration (Lewis, Walkey & Dartnall, 1972; Crawford, 1974). Ninespine stickleback also tolerate high salinity (Nelson, 1968). These adaptations allow sticklebacks and blackfish to overwinter in lakes where other species cannot. This is especially the case for the Alaska Blackfish, which may be more tolerant due to its air-breathing capabilities and

resistance to extreme cold (Scholander *et al.*, 1953). The occupancy models showed that Alaska blackfish were more likely to be found in lakes with more deep-water refugia, probably because they overwinter in these lakes. Conversely, slimy sculpin may be less tolerant of winter conditions than sticklebacks and blackfish. This disparity in tolerance may restrict slimy sculpin to areas with large amounts overwintering habitat (Hershey *et al.*, 2006), which is reflected in their restricted distribution and low occupancy rates. If these refugia also harbour overwintering piscivores, this may further affect slimy sculpins through predation (Hanson, Hershey & McDonald, 1992).

As ice melts during spring, fish occupancy becomes less dependent on deep-water refugia (Fig. 3). Rapid thawing is accompanied by a spring freshet, causing an increase in water level, widespread flooding and an overall increase in landscape connectivity. Lakes become connected temporarily, at which point undirected dispersal is an important driver of fish occupancy for small-bodied species, particularly those capable of rapid recolonisation of depopulated lakes. Although movement capabilities and body size are generally positively related (De Bie *et al.*, 2012), the small size of Alaska blackfish and ninespine stickleback may aid their dispersal through ephemeral pathways in early spring. Many of these connections are temporary and shallow, do not have directional flow and are potentially difficult to navigate for larger-bodied species. The number of ephemeral connections peaks in the spring and declines thereafter (Fig. 3). However, ephemeral connections may continue to act as dispersal conduits for small-bodied species through the summer; young or adults may disperse opportunistically at times of high water. This may be particularly true in landscapes where lakes are close together and may occasionally become connected. Perhaps for this reason, Alaska blackfish were more likely to be found in areas where lakes were close together.

Alaska blackfish are physiologically tolerant of winter conditions, possessing an air-breathing organ allowing them to use atmospheric oxygen (Crawford, 1974), including that trapped under the ice of frozen lakes (Campbell *et al.*, 2014). Such specialist adaptations and limited dispersal capabilities suggest that tolerance explains their persistence. Ninespine sticklebacks, in contrast, may be less tolerant than blackfish but appear to have a dispersal and recolonisation capability characteristic of an opportunistic life history (Winemiller & Rose, 1992). It seems possible that the stickleback is widely distributed in the Arctic largely due to its ability rapidly to recolonise depopulated lakes via shallow and

ephemeral connecting waterbodies, indicating that the stickleback is resilient rather than tolerant. The ninespine stickleback has a short generation time, grows quickly and can reach high population density quite rapidly (Cameron, Kostoris & Penhale, 1973). They were often caught in large numbers; in some lakes, a 12-h fyke net set would catch more than 10 000 individuals (100-fold greater than the maximum Alaska blackfish catch-per-unit-effort). Such high density may make dispersal more likely, and the latter is perhaps density dependent. Although stickleback dispersal has not been studied directly in this region, Cameron *et al.* (1973) noted major population movements at the beginning of the growing season at a single lake, supporting our speculation that sticklebacks use the spring freshet for dispersal and recolonisation.

The spring freshet is also important for large-bodied migratory species. Formerly frozen rivers and streams begin to flow and connect overwintering and summer foraging habitats (Fig. 3). Large-bodied species demonstrate characteristics of a 'periodic' life history (Winemiller & Rose, 1992; Miyazono *et al.*, 2010); in summer, they migrate from overwintering habitats into connected systems. This may have been reflected in the occupancy patterns of large-bodied species, which was associated with local lake connectivity. Least cisco, broad whitefish and arctic grayling have a strong ability to colonise lakes with connections that remain wet through the growing season, but not lakes with only ephemeral connections. The spatial arrangement and composition of landscape features are also important and can affect colonisation potential beyond direct measures of connectivity alone (Dunning, Danielson & Pulliam, 1992). We found that the broad whitefish was more likely to occur in regions where lakes were spaced closer together. Although we initially categorised the L_DistLake variable as related to undirected dispersal, it may also be important for migratory species, which can use lakes as migratory stepping stones. Least cisco and broad whitefish were more likely to be found in lakes closer to the north coast, which allows better access to the marine feeding and overwintering habitat (Reist & Bond, 1988).

The probability of occupancy for least cisco was also positively related to local habitat features, including lake size and availability of overwintering refugia. These features may be more important for least cisco than for other large-bodied species, because least cisco may have a resident form. Least cisco can have riverine, anadromous and lacustrine forms (Reist & Bond, 1988), and thus, certain populations of least cisco may overwinter

in large lakes with deep-water refugia. If least cisco are permanent residents in some lakes on the ACP, it would explain the importance of deep-water refugia and lake size for them but not other large-bodied species. It might be that all three large-bodied species move into lakes during the summer to feed and then leave for winter refugia in streams and rivers, which can be widespread on the ACP (Huryn *et al.*, 2005), or in the sea. However, if a connected lake becomes isolated due to changes in the stream network, migratory fish may become trapped in a lake (Hershey *et al.*, 2006). If this occurs, least cisco may survive if suitable overwintering habitat is present. In support of this, we found least cisco was the most widely distributed of the large-bodied species in our study and occurred in the widest range of habitats, including nine lakes without obvious connections (in seven of which we captured young-of-the-year least cisco).

During summer, ephemeral connections dry up, and thus, we hypothesise a decline in the importance of undirected dispersal for lake occupancy (Fig. 3). As summer progresses and lakes warm, deep-water refugia may again increase in importance by providing cool water for cold stenotherms, such as whitefish (e.g. Jacobson *et al.*, 2011). The increase in importance of deep-water refugia continues into late summer/early autumn as fish face an increasing risk of isolation in unsuitable overwintering habitat before freeze-up. During early autumn, there is presumably a pulse of fish movement as migratory species move to the rivers or marine overwintering habitat. Because some ephemeral connections are re-established by autumn rain, there is also a brief opportunity for undirected dispersal, especially for ninespine sticklebacks. By late autumn lakes, streams and rivers begin to freeze again, restricting fish movement and increasing once more the importance of deep-water refugia for overwintering fish.

Because winter conditions cause local extinction in many lakes, fish occupancy on the ACP in the winter may be similar to other systems where extinction or niche partitioning is more important than colonisation in shaping distributions (e.g. Magnuson *et al.*, 1998; Warfe *et al.*, 2013). Many lakes may be suitable during the summer but cannot sustain fish populations over the winter. Migratory species move out of these habitats before winter and other species which dispersed into these habitats and establish populations in the summer are unlikely to survive. For example, ninespine sticklebacks were found in four lakes without overwintering habitat (i.e. 0% of the lake area is over 2 m in depth). These shallow lakes are probably population sinks for rapid dispersers such as ninespine

stickleback (Olden, Jackson & Peres-Neto, 2001). However, if these shallow lakes are connected, they may be temporary habitat for migratory species (e.g. least cisco were also found in two of these four shallow lakes that had connections). If we were to examine lake occupancy during the winter, we would undoubtedly find a more restricted distribution for all species. Further, because winter conditions are likely to affect species differently, species relative occupancy rates would change. For example, because blackfish have more physiological adaptations for winter conditions, they may be more widespread during winter compared with ninespine stickleback. Thus, we hypothesise that the importance of local persistence alternates with that of colonisation potential, the magnitude of that change depending on species.

We used a knowledge of fish distribution patterns to provide insight into how fish species are able to persist in the harsh and dynamic environment of the Arctic Coastal Plain. Given that this is a large region, encompassing tens of thousands of lakes, ponds and wetlands, future work should aim to expand and test these hypotheses using both species distribution and life-history studies. Additionally, examination of fish distribution at the assemblage level is needed to determine which of the factors we have identified (or may have missed) are driving patterns in species richness. Given the strong effects of variables such as connectivity (during the growing season) and deep-water refugia (during winter), species richness may be primarily shaped by these factors (e.g. Olden *et al.*, 2001) which could result in two or three distinct fish assemblages (e.g. Mehner *et al.*, 2005). Lastly, the environmental variables identified here as organising factors of fish distribution can serve as the basis of hypotheses to be tested by molecular markers. Have widespread lake connectivity and frequent dispersal led to homogenous patterns of genetic variation across the ACP for some species? Genetic assessments would also permit inference of how past populations of Arctic fish have responded to historical climate perturbations, thus yielding insights into how their distributions may respond to future change (e.g. Hope *et al.*, 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Model ranking based on Akaike's information criterion adjusted for sample size and overdispersion (QAICc), differences in QAICc (ΔQAICc), model weight, model likelihood and number of parameters (K) for the single-season model of occupancy for Alaska blackfish in lakes on the Arctic Coastal Plain, Alaska

Table S2. Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood and number of parameters (K) for the single-season model of occupancy for slimy sculpin in lakes on the Arctic Coastal Plain, Alaska

Table S3. Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood and number of parameters (K) for the single-season model of occupancy for least cisco in lakes on the Arctic Coastal Plain, Alaska

Table S4. Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood and number of parameters (K) for the single-season model of occupancy for broad whitefish in lakes on the Arctic Coastal Plain, Alaska

Table S5. Model ranking based on Akaike's information criterion adjusted for sample size (AICc), differences in AICc (ΔAICc), model weight, model likelihood and number of parameters (K) for the single-season model of occupancy for arctic grayling in lakes on the Arctic Coastal Plain, Alaska

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